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**A Late Miocene Marlin, *Makaira* sp. (Perciformes, Osteichthyes)
from San Diego County, California, U.S.A.**

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Abstract. Fossil bones collected in the latest Miocene (= either late Clarendonian or early Hemphillian North American Land Mammal Age), San Mateo Formation, near Oceanside, San Diego County, California, U.S.A., belong to a single specimen of the genus *Makaira*, species undetermined, and is part of the San Luis Rey River Local Fauna. For the genus, this represents the fifth discovery in fossil deposits bordering or within the Pacific Ocean region, and the third discovery in southern California. The specimen is within the known geochronological distribution of the genus (Late Miocene to Recent), provides further evidence that the coastal palaeoclimate of southern California was warmer than at present, and indicates that there probably was a deep water, oceanic habitat at or near the depositional site.

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INTRODUCTION

Fossil marlins of the genus *Makaira* Lacépède 1802 (Class Osteichthyes, Order Perciformes, Family Istiophoridae) are known from four localities bordering or within the Pacific Ocean. These marlins include the Late Miocene *M. panamensis* Fierstine 1978, from Panama, *Makaira* sp. from two Late Miocene localities near El Toro, California (Fierstine & Applegate, 1968), and an Early Pleistocene *M. indica* (Cuvier, 1832) from Luzon, Philippines (Fierstine & Welton, 1983). Although there is some nomenclatorial controversy (Nakamura, 1983), only two species of the genus *Makaira* (the black marlin, *M. indica*, and the blue marlin, *M. nigricans* Lacépède 1802) are generally considered to inhabit the tropical and temperate regions of the Indo-Pacific Ocean today (Robins & De Sylva, 1960). The fossil discoveries are within the known geographic range of distribution of the extant species of *Makaira* (Fierstine & Welton, 1983).

In their description of the San Luis Rey River Local Fauna (San Mateo Formation, latest Miocene, Oceanside, California), Barnes *et al.* (1981) mentioned the discovery of associated bones of a single individual marlin of large size. This represents a significant find because it not only adds one more specimen to a very poor fossil record for marlins, but allows analysis of several bones (e.g. articular, dentary, preoperculum, and pterygiophores) that have not been collected with any of the other fossil marlin specimens.

The following study is a description of the marlin from the San Luis Rey River Local Fauna and its comparison to other fossil and living istiophorids, particularly marlins of the genus *Makaira*.

MATERIALS

Abbreviations: HLF = collection housed at California Polytechnic State University, San Luis Obispo; LACM = Natural History Museum of Los Angeles County; USNM/BRUUN = United States National Museum of Natural History, Anton Bruun cruise; UCLA = University of California at Los Angeles; UCMP = University of California Museum of Paleontology, Berkeley.

Comparative Recent material: HLF 118: *Istiophorus platypterus* (sailfish), entire skeleton, off Stradbroke Id., Queensland, Australia, size, sex, and weight unknown; HLF 106: *M. indica* (black marlin), entire skeleton, off Cairns, Queensland, Australia, 256.5 cm body length (lower jaw to fork of tail), male, 90 kg; USNM/BRUUN

565-60: *M. nigricans* (blue marlin), entire skeleton, 18°28'S, 83°19'W, 272 cm body length, female, weight unknown; HLF 114: *M. nigricans*, skull, off Kona, Hawaii, U.S.A., 274 cm body length, female, 159.9 kg; HLF 135: *M. nigricans*, rostrum and partial lower jaw, off Kona, Hawaii, U.S.A., body length unknown, female, 295.2 kg; UCLA/S281: *Tetrapturus audax* (striped marlin), axial skeleton, eastern Pacific Ocean, size, sex, and weight unknown.

SYSTEMATIC DESCRIPTION

Class	Osteichthyes
Order	Perciformes
Suborder	Scombroidei
Family	Istiophoridae

Makaira sp.

Referred material: UCMP 118559, partial associated skeleton consisting of nearly complete abdominal vertebra, partial pterygiophores 1 and 2 of first dorsal fin, left articular, left dentary with complete tooth row, right lower tooth row fragment, right nearly complete hyomandibular, right ventral hypohyal, partial right operculum, partial left operculum, left postcleithrum 1, partial left preoperculum. All material was collected over a four-year period (1974 to 1978) by at least three different people.

Locality: The fossil material was collected from a fine grained, greenish-grey sand at locality UCMP V68147 (= LACM 4297) in Oceanside, San Diego County, California, U.S.A. According to Domning & Deméré (1984), this locality is in a basal rock unit within the marine San Mateo Formation and is either late Clarendonian or early Hemphillian in age (latest Miocene between approximately 7 and 9 million years old). The faunal aggregate is named the San Luis Rey River Local Fauna (Barnes *et al.*, 1981) and contains sharks, bony fishes, birds, and mammals (both marine and terrestrial).

Description: Unless noted otherwise, the following fossil elements are indistinguishable in morphology from their homologues in either *M. indica* or *M. nigricans*.

The single abdominal vertebra (Text-fig. 1B) is similar to the sixth abdominal vertebra of modern istiophorids with regard to the general shape and size of the neural spine and zygapophyses, and the placement of the rib facet. When the ratio of the width of the anterior face of the centrum to the length of the centrum is compared between four extant species (Table 1), the fossil specimen is most similar to *M. indica* and *M. nigricans*.

The left articular (Text-fig. 1E and F) is larger (56.4 mm, greatest depth) than any material available for comparison. The funnel-shaped fossa for the articulation of the quadrate has a longitudinal groove (gr, Text-fig. 1F) at the base of its medial process. This feature is present in *M. indica* (HLF 106), but is lacking in *M. nigricans* (HLF 114 and USNM/BRUUN 565-60).

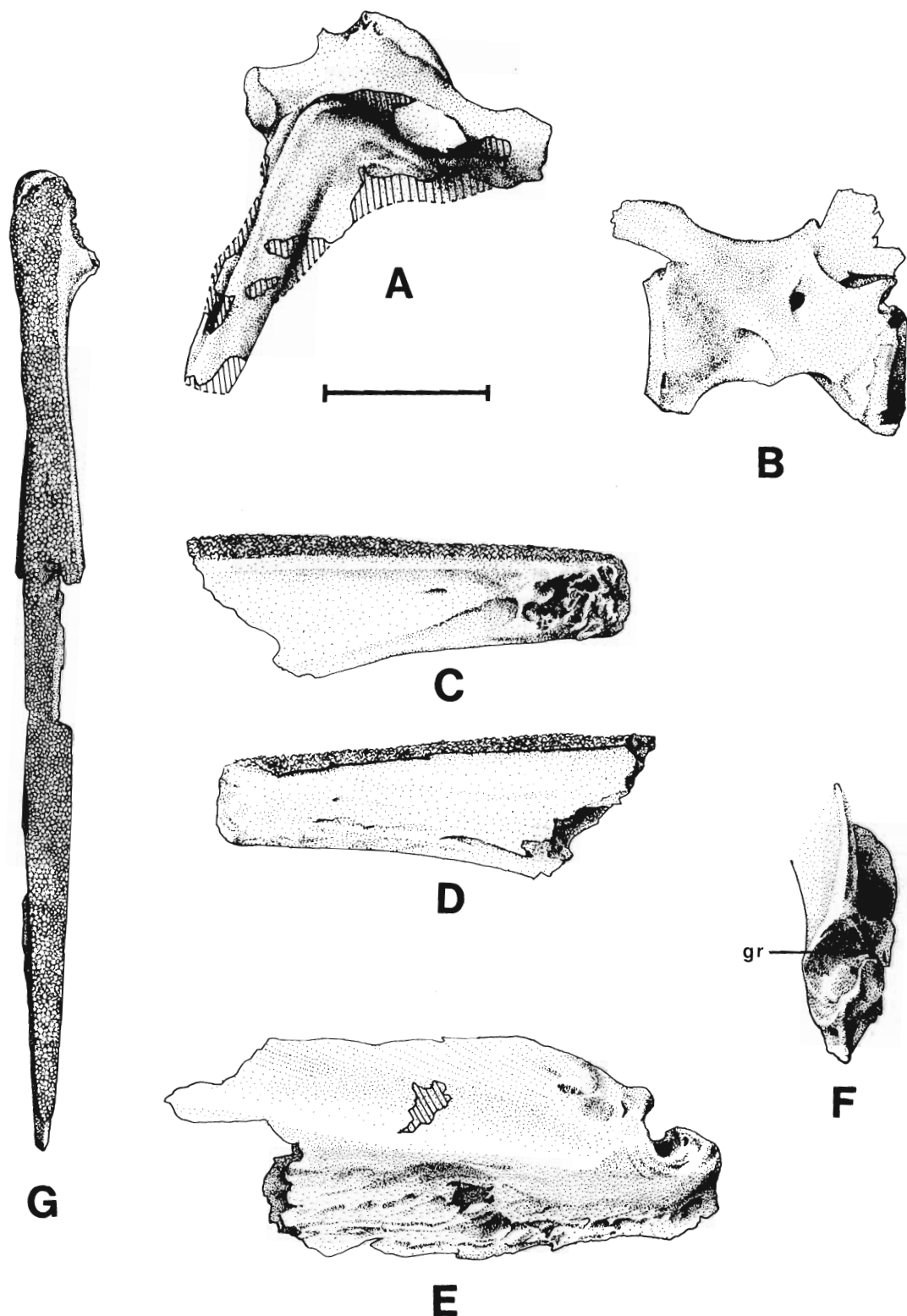
The left dentary consists of a large distal fragment (Text-fig. 1C and D) and a tooth row fragment that together form a nearly complete left tooth row (Text-fig. 1G) 295 mm long. This tooth row is longer than any comparative material on hand. For example, in *M. nigricans*, the right tooth row of HLF 135 is 270 mm long (the left tooth row is incomplete) and the left tooth row of USNM/BRUUN 565-60 and of HLF 114 measure 245 mm and 270 mm, respectively.

The right hyomandibular (Text-fig. 1A) is 95.6 mm wide (from opercular process to sphenotic process) and 126.8 mm long (pteric process to distal articulation with symplectic). It is similar in size and morphology to the hyomandibular of *M. nigricans* (USNM/BRUUN 565-60).

The right dentary (not illustrated) is represented by a proximal tooth row fragment (56.3 mm long) which is identical in size and shape to its homologous area in the left tooth row.

Pterygiophores 1 and 2 of the dorsal fin (not illustrated) measure 32.5 mm and 40.0 mm, respectively, across the base. The proximal part of each pterygiophore is missing. Each fossil pterygiophore is slightly smaller than similar elements in the dorsal fin of *M. nigricans* (USNM/BRUUN 565-60).

The right ventral hypohyal (not illustrated) measures 66.5 mm long and 42.9 mm high and is longer than the same element in USNM/BRUUN 565-60 (57.1 mm × 43.5 mm).



Text-figure 1. *Maikara* sp., UCMP 118559, from locality UCMP V68147 (= LACM 4297), San Mateo Formation (latest Miocene), Oceanside, San Diego County, California. A, Right hyomandibular, lateral view; B, Abdominal vertebra, left lateral view; C, Left dentary, medial view; D, Left dentary, lateral view; E, Left articular, lateral view; F, Posterior region of left articular showing funnel-shaped fossa for articulation with quadrate and longitudinal groove (gr), postero-dorsal view; G, Nearly complete tooth row of left lower jaw, dorsal view; anterior is toward top of page. Cross-hatch indicates missing areas. Scale equals 50 mm.

Both right and left opercula (not illustrated) are each represented by a fragment that contains the fossa for articulation with the hyomandibular. Both specimens are of similar size and morphology, but their fragmentary nature makes comparison with the extant species very difficult. The fossa of the right operculum articulates perfectly with the right hyomandibular fragment (Text-fig. 1A).

The left preopercular fragment (not illustrated) is missing its dorsal-most tip, the postero-ventral segment and much of its posterior and ventral margins. It is similar in size to the left preoperculum of *M. nigricans* (USNM/BRUUN 565-60).

The left postcleithrum 1 (not illustrated) is nearly complete and has a surface for articulation with postcleithrum 2 that is approximately 50% of the length of the entire bone. The left postcleithrum 1 of *M. nigricans* (USNM/BRUUN 565-60) has an articular surface that is 33% of its length and *M. indica* (HLF 106) has one that is 27%.

These differences in lengths of the articular surfaces probably have no systematic value because there seems to be a general lack of right-to-left symmetry in the postcleithra of the two extant species. For example, the right postcleithrum 1 of *M. nigricans* (USNM/BRUUN 565-60) is longer than the left and has an articular surface that is approximately 50% of its length. The right postcleithrum 21 of *M. indica* (HLF 106) is slightly longer (7.5%) than the left, however its articular surface ratio (26%) is nearly identical to the left (27%).

DISCUSSION AND CONCLUSIONS

Based upon the ratio of the length to width of the abdominal vertebra (Table 1) and the size of the other elements, the fossil fish is probably a marlin of the genus *Makaira*, although it cannot be assigned to either of the two extant species (*M. indica* or *M. nigricans*), or one extinct species (*M. panamensis*). Osteological differences between these three species are based upon the neurocranium, rostrum, and pectoral fin (Fierstine, 1978; Fierstine & Welton, 1983; Nakamura, 1983), material not represented in this fossil specimen.

Species (Collection Number)	Length of centrum	Width of anterior face of centrum	Ratio of centrum length to width
<i>Istiophorus platypterus</i> (HLF 118)	70.6	32.8	.46
<i>Tetrapturus audax</i> (UCLA/S281)	55.5	29.9	.54
<i>Maikara nigricans</i> (USNM/BRUUN 565-60)	70.0	47.0	.67
<i>Maikara indica</i> (HLF 106)	54.3	36.9	.68
Fossil <i>Makaira</i> sp. (UCMP 118559)	73.7	50.9	.69

Table 1. Selected measurements (in millimetres) of the 6th abdominal vertebra of four extant species of billfish and the fossil *Makaira* sp. (UCMP 118559).

All bones (UCMP 118559) are believed to be from the same individual since they were found at one site and there was no duplication among the 12 bony elements. This conclusion agrees with the original observation by Barnes *et al.* (1981).

Since the hyomandibular and preoperculum of UCMP 118559 are similar in size to a *M. nigricans* (USNM/BRUUN 565-60) with a body length of 272 cm, then it is probable that the fossil marlin had a similar body length. According to length-weight curves in Skillman & Yong (1974), individuals of *M. indica* or *M. nigricans* of this size would weigh approximately 125 kg.

When compared to the two extant marlins of the genus *Makaira*, it is unlikely the fossil marlin (UCMP 118559) has a longer lower jaw than expected for an animal of its size. *M. nigricans* has a maxillary length (which approximates lower jaw length) 14.0-15.9% of the body length and *M. indica* has a maxillary length 11.9-15.3% of the body length (Nakamura, 1983). These data yield an intraspecific variation of 1.9% for *M. nigricans* and 3.4% for *M. indica*. Assuming the fossil marlin is the same body length (272 cm) as USNM/BRUUN 565-60 (*M. nigricans*), then the left lower tooth row (29.5 cm) is 10.8% of its body length, whereas the lower tooth row (24.5 cm) of USNM/BRUUN 565-60 is 9% of its body length. If one assumes that the length of the tooth row on the dentary when compared to body length varies similarly to the values for maxillary length, then the 1.8% difference between the fossil marlin and USNM/BRUUN 565-60 is within the expected intraspecific variation.

The genus *Makaira* has been identified in the Late Miocene of southern California (El Toro, Orange Co.) on the basis of a partial rostrum and a prementary bone (Fierstine & Applegate, 1968). The specimen from the San Luis Rey River Local Fauna documents another occurrence of the genus in southern California, but it adds little to our chronological knowledge, since the genus was already known to have a geochronological range from Late Miocene to Recent.

If one assumes that the fossil marlin has ecological requirements similar to the extant *M. indica* and *M. nigricans*, then its discovery helps solve differences in interpretation of the depositional environment of the San Luis Rey River Local Fauna (Barnes *et al.*, 1981; Domning & Deméré, 1984). Both *M. indica* and *M. nigricans* are oceanic, warmwater species that usually live over deep water. Both species have similar surface temperature optima, 23-24°C (Nakamura, 1975; Rivas, 1975). Although there are published records of them as far as 35°N in the eastern Pacific ocean (Nakamura, 1974, 1983), extant members of both species are considered to be rare off southern California (Eschmeyer *et al.*, 1983). Based on the presence of flightless auks, anadromous salmon, pin-nipeds and land mammals in the same horizon, as well as geologic evidence, Barnes *et al.* (1981) concluded that the San Luis Rey River Local Fauna was deposited nearshore, probably near a mouth of a major river. This is an unlikely environment for extant *M. indica* or *M. nigricans*. Basing their conclusion primarily on geologic evidence, Domning & Deméré (1984), believe the rock unit containing the San Luis Rey River Local Fauna was deposited under "normal" marine conditions, perhaps at middle to inner depths of the continental shelf. The presence of *Makaira* sp. in the fauna favours the deeper, more oceanic interpretation.

In obvious contrast to living individuals, it is not unusual for fossil specimens of the genus *Makaira* to be associated with organisms from different habitats. Meyer *et al.* (in press) described *M. calvertensis* (Berry, 1917) from the Early Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A. Basing their decision on the most abundant otoliths, Fitch & Lavenberg (1983) postulated that the fauna in the Yorktown formation may represent deposition at 60 to 100 m, even though it contains otoliths from fish that seldom stray into depths greater than 6 m. One of us (H.L.F.) is studying a rostrum from a large marlin (*Makaira*) from the Middle Miocene Gatún Formation, Panama where there is an associated fauna that contains a mixture of marine vertebrates from coastal to open-water habitats (Gillette, 1984).

We are not certain why marlins are in these mixed marine assemblages. The extinct great white shark, *Procar-charodon megalodon* (Agassiz, 1843), is present in the San Luis Rey River Local Fauna (Domning & Deméré, 1984), the Gatún Formation (Gillette, 1984), and the Yorktown Formation (Meyer *et al.*, in press). Perhaps marlins were transported to some depositional sites as stomach contents of large predators or by ocean currents if they were dead or dying.

If our identification is incorrect and the fossil bones belong to a large specimen of the striped marlin, *Tetrapturus audax* (Philippi, 1887) or to some unknown species, then a marlin's presence in the San Luis Rey River Local Fauna becomes less enigmatic. In the eastern Pacific Ocean, *T. audax* is present throughout the year from 30°N to 30°S and supports a large sport fishery off southern California between August and October (Ueyanagi & Wares, 1975). Although usually found in an oceanic, off-shore habitat, *T. audax* may be found in coastal waters (Eschmeyer *et al.*, 1983). However, *Tetrapturus* and *Makaira* are distinguished in part by differences in the morphology of their vertebrae (Nakamura, 1983), and we have no reason to question our identification of the fossil marlin.

This third record of the genus *Makaira* in Late Miocene deposits of southern California, indicates that marlins were more common then off southern California than they are today and that the seas were much warmer. This conclusion agrees with the reconstruction of California coastal palaeoclimates as suggested by Addicott (1970), Domning (1978), and Durham (1950).

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